

Feeding Behavior in Three Species of Sharks¹

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THIS REPORT concerns a study of the feeding behavior in three species of sharks: *Carcharhinus menisorrhoeus* Müller and Henle, the grey shark (Fig. 1), *Carcharhinus melanopterus* Quoy and Gaimard, the blacktip shark (Fig. 2), both of the family Carcharhinidae; and *Triacodon obesus* Rüppell, the whitetip shark (Fig. 3), of the family Triakidae. The study was conducted in the lagoon at Eniwetok Atoll, Marshall Islands, during the summers of 1959 and 1960. It was a segment of a broad program of investigation of shark behavior in which laboratory and field work were coordinated whenever possible. The overall program, conducted at both the Eniwetok Marine Biological Laboratory and the Hawaii Marine Laboratory, Coconut Island, Hawaii, was under the direction of Dr. Albert L. Tester, with financial support from the Office of Naval Research (Contract Nonr 2756(00), Project NR 104503).

Observations of sharks in their natural environment have been the basis for most of the shark literature which is available today and yet comparatively little has been offered toward a realistic understanding of shark behavior. Most of this material has been written for popular consumption and is therefore oriented toward the sensational rather than the scientific.

We do find scientifically oriented accounts in the literature (as for example, Eibl-Eibesfeldt and Hass, 1959; Limbaugh, 1958; and Wright, 1948) but these observations are limited largely to incidental encounters.

A critical study of shark behavior, undertaken with planned experiments in the sharks' natural

environment—the aim of this investigation—has been almost completely neglected.

In this study, a comparison is made of the feeding behavior of the three species. Behavior is further related to habitat and to distribution within the lagoon. Experiments designed to illustrate the roles played by the major sensory modalities are presented. This last portion of the investigation, dealing primarily with grey sharks, includes a consideration of the specific stimuli involved in releasing feeding behavior. Consideration is also given to food preferences and to factors which may possibly inhibit feeding.

GENERAL DESCRIPTION OF STUDY AREAS

The study was centered about two primary locations: (1) the lee of Engebi Island during 1959, and (2) the lee of Bogen Island, adjacent to Deep Channel, during 1960. The Engebi Island site was in 15 ft of water over a relatively shallow sand and coral rubble flat extending out from shore for approximately 400 yd before dropping suddenly into the deeper regions of the lagoon. Currents are weak in this area and the water is generally turbid, with underwater visibility commonly less than 20 ft. At the Bogen Island site strong tidal currents are present and underwater visibility often exceeds 100 ft. The edge of Deep Channel at this point drops abruptly from a depth of approximately 10 ft at the rim to 110 ft at the bottom.

At these locations, observations were made from the following vantage points:

1. An underwater chamber was fitted to a vessel moored in the lagoon. This chamber was a metal cylinder, 14 ft long and 2½ ft in diameter, open at the top and closed at the bottom, with viewing ports on three sides near the bottom. An observer in the chamber was situated approximately 8 ft below the surface.

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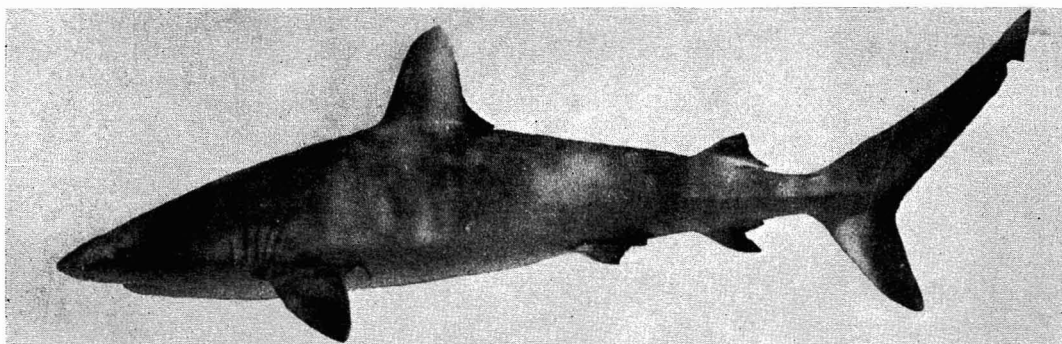


FIG. 1. The grey shark, *Carcharhinus menisorrhah*. (Photo by E. Hobson.)

2. A wire cage was suspended from a raft anchored on the slope at the edge of Deep Channel. An observer in this cage was located immediately below the surface.

3. A canvas screen, anchored on the bottom, concealed an observer lying prone on the bottom wearing SCUBA equipment.

4. A 16-ft glass-bottom boat, having the added advantage of mobility, provided for observations of activity directly below.

5. In many cases, the observations involved incidental encounters with sharks during the course of such routine underwater activity as installing apparatus, etc.

Experimental procedures and apparatus will be further described as they pertain to the report.

SPECIES STUDIED

Identification of the sharks is based on Schultz et al (1953). All three species, *Carcharhinus menisorrhah*, *C. melanopterus*, and *Triaenodon obesus*, reportedly have a wide Indo-Pacific distribution. They are reported from the Red Sea as well as the Maldive Islands by Klauswitz (1958, 1959). Although positive identification of the two carcharinids awaits a revision of the family on a world-wide basis, all three species appear to be prominent in the shark populations of most Pacific atolls. Harry (1953) reports them from the Tuamotus, as does Randall (1955) from the Gilbert group. The author found them abundant at Palmyra and they were the only species of sharks consistently seen in the lagoon at Eniwetok during the present investigation.

GENERAL OBSERVATIONS OF BEHAVIOR

Often when we were engaged in various types of activity in the lagoon the resulting commotion, which commonly involved splashing on the surface or striking metal tools on hard objects underwater, was immediately followed by the rapid approach of an obviously alerted blacktip or grey shark.

In spite of this initial attraction to many stimuli, both species exhibited varying degrees of caution when encountering unfamiliar situations. This was particularly apparent in the blacktip, a species which seemed especially sensitive to potential danger. When work was begun at Engebi, blacktips often circled at the limit of visibility in the baited area for as long as 2 or 3 hr before approaching the bait. Then, when an approach was made, it seemed to be done reluctantly and was often cut short by some stimulus, unnoted by the observer, which startled the shark as it neared the bait and caused it to swim rapidly away. Usually the shark repeated the approach, but in these early tests it was not until several sharks had become active in the area that a blacktip finally took the bait. We subsequently found that we were dealing with the same blacktips day after day at Engebi and that as the work progressed, their initial caution steadily declined. This was presumably due to a growing familiarity with the situation. Nevertheless, a month of testing passed before the blacktips took the bait without hesitation. Once released, the attack of the blacktip was very fast and aggressive.

The grey was a notably bolder species. Al-

though a blacktip often approached rapidly in response to splashing at the surface, it then generally reversed direction and retreated just as rapidly if the investigation of the splashing brought it into an encounter with a human. In the same situation, the grey ordinarily reacted to the encounter with a human by continuing the approach to approximately 5 yd from the human, at which point it would veer aside and circle with an apparent cautious interest. If no further stimuli were introduced, the grey moved on.

Blacktips and greys showed a marked increase in excitement when feeding in numbers. This phenomenon, generally referred to in extreme cases as the feeding frenzy, has been observed in many species of sharks. In the blacktips and greys, the presence of more than one shark appeared to lower the threshold for the release of feeding behavior.

Whitetips did not show this group effect. Even when feeding in numbers, members of this species responded individually and without a notable increase in excitement. The whitetip seemed to be relatively unresponsive to many of the stimulus situations which elicited a sharp reaction in the grey and blacktip. There was little overt response seen in this shark when encountering a human in the water for the first time. In this situation we did not see the curiosity frequently exhibited by the greys, nor the start and rapid flight usually exhibited by the blacktip.

On several occasions whitetips appeared and

took fish from the spears of divers before the fish could be removed from the water. Even in these instances, the slow, deliberate actions of this shark did not give the impression of being a threat to the diver. This impression may have been an illusion based on the sluggish behavior of the animal. On one such occasion a 6-ft whitetip bit the fish in half and then made a slow pass at the diver holding the other end of the spear. This appeared to be a warning pass at a potential competitor rather than an active attack. Such warning passes were noted on several occasions directed at grouper or snappers which approached a bait that was under attack by a whitetip. Similar behavior was noted in greys and blacktips. Tester (personal communication) observed a small blacktip pursue a grouper of comparable size from a bait which had been placed on the bottom in shallow water near Aniyaani Island. In this case, the blacktip showed considerably more than a warning pass as it actively pursued the grouper among a concentration of small coral heads. We did not observe these sharks exhibiting aggressive behavior toward members of their own species. One observation made on numerous occasions might at first glance seem to oppose this view. When a bait which was too large to be immediately swallowed was presented to a group of feeding greys or blacktips, the shark which succeeded in taking the bait would invariably swim rapidly away from the area, shaking its head vigorously from side to side presumably in attempts at cutting up and swallowing the bait. As it fled,

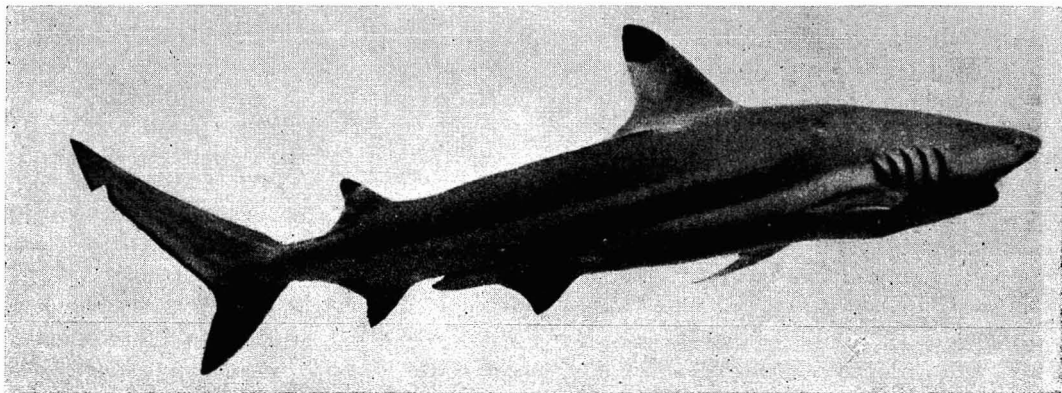


FIG. 2. The blacktip shark, *Carcharhinus melanopterus*. (Photo by E. Hobson.)

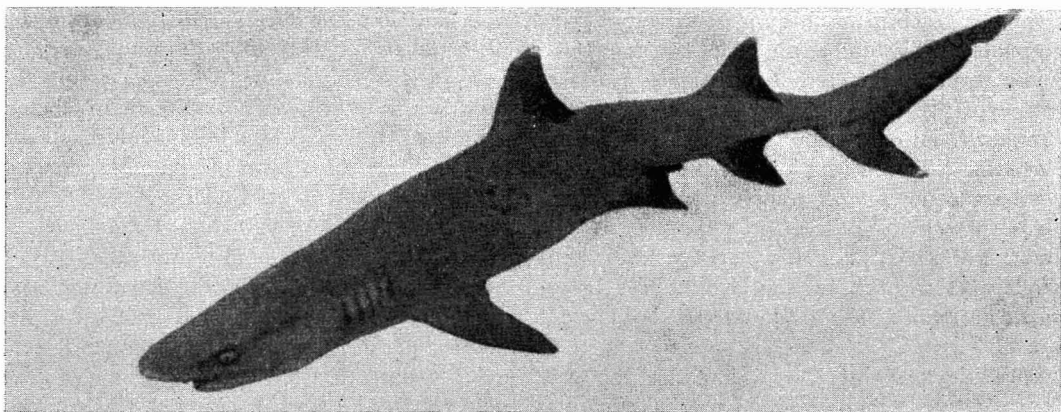


FIG. 3. The whitetip shark, *Triaenodon obesus*. (Photo by E. Hobson.)

the other sharks always followed in close pursuit. Although the flight of prey was commonly noted to release attack in the grey, the aggressive behavior of these other sharks in this case was believed to have been directed against the bait rather than the fleeing shark.

There was never any mistaking an alerted grey or blacktip from one engaged in normal patrolling activity. Thus we had no difficulty distinguishing a grey or blacktip entering the test area in response to a stimulus situation we had presented from one incidentally passing through the area. The movements of the alerted greys and blacktips were markedly accelerated and the grey in particular seemed tense and highly responsive to subsequent stimulation. Movements of the grey immediately before attack were markedly abrupt; its body often appeared stiff, with back slightly arched and head extending straight out and slightly upward. The pectoral fins were characteristically pointed noticeably downward. Attack was prefaced in many cases by such anticipatory movements as a lateral shaking of the head (noted also by Eibl-Eibesfeldt and Hass, 1959) and a movement of the jaws as in biting (Hobson et al., 1961).

Although it was not always so easy to make this distinction with the seemingly unresponsive whitetip, these sharks were undoubtedly more responsive than they appeared to be. It is likely that their reactions were simply more subtle than those of the more excitable greys and blacktips. Whitetips usually appeared in

an area shortly after divers had undertaken various types of underwater activity. However, after their appearance the whitetips would swim about without any apparent interest in the proceedings. Nevertheless, the consistency of these appearances indicated that the sharks sensed activity and were interested.

DISTRIBUTION OF SPECIES WITHIN LAGOON

Blacktips were the most commonly observed shark over the sand and coral rubble flats lying under approximately 1–40 ft of water at the perimeter of the lagoon. These flats extend out from shore for distances ranging from approximately 50 yd to several miles before the bottom falls off sharply into the depths. Coral growth in this area is generally restricted to large isolated heads which, in many cases, reach the surface of the water at low tide. Although blacktips exceeding 6 ft in length were seen, specimens of more than 4 ft were not common. Small blacktips were very common on the seaward reef flats when the sea covered these flats at high tide. The seaward flats were largely exposed at low tide.

The whitetip also frequented the shallow waters of the lagoon, although unlike the blacktip, which foraged widely over the flats, the whitetip centered its activity among the coral heads and about the coral-rock ledges which border the seaward passages. Unlike the other two species, the whitetip was commonly seen resting motionless on the bottom, often under

ledges and in caves. The whitetip was common to a length of 6 ft, with individuals of 7 ft seen on occasion.

We seldom encountered the blacktip when we moved down the slopes from the shallow flats into the deeper waters of the lagoon or seaward passages, but here we found the grey shark in abundance. A census of the shark popu-

lation of the entire lagoon would probably show the grey shark to be the most numerous. This shark was commonly seen up to 7 ft in length.

All three species were generally observed swimming close to the bottom unless drawn toward the surface to feed.

Figure 5 shows shark sightings by species during a period of 30 days in the vicinity of



FIG. 4. The test area off Bogen Island, showing the relative position of Deep Channel (top), raft (at edge of channel), and the barge. The island is out of the picture to the left. (Photo by R. A. Boolootian.)

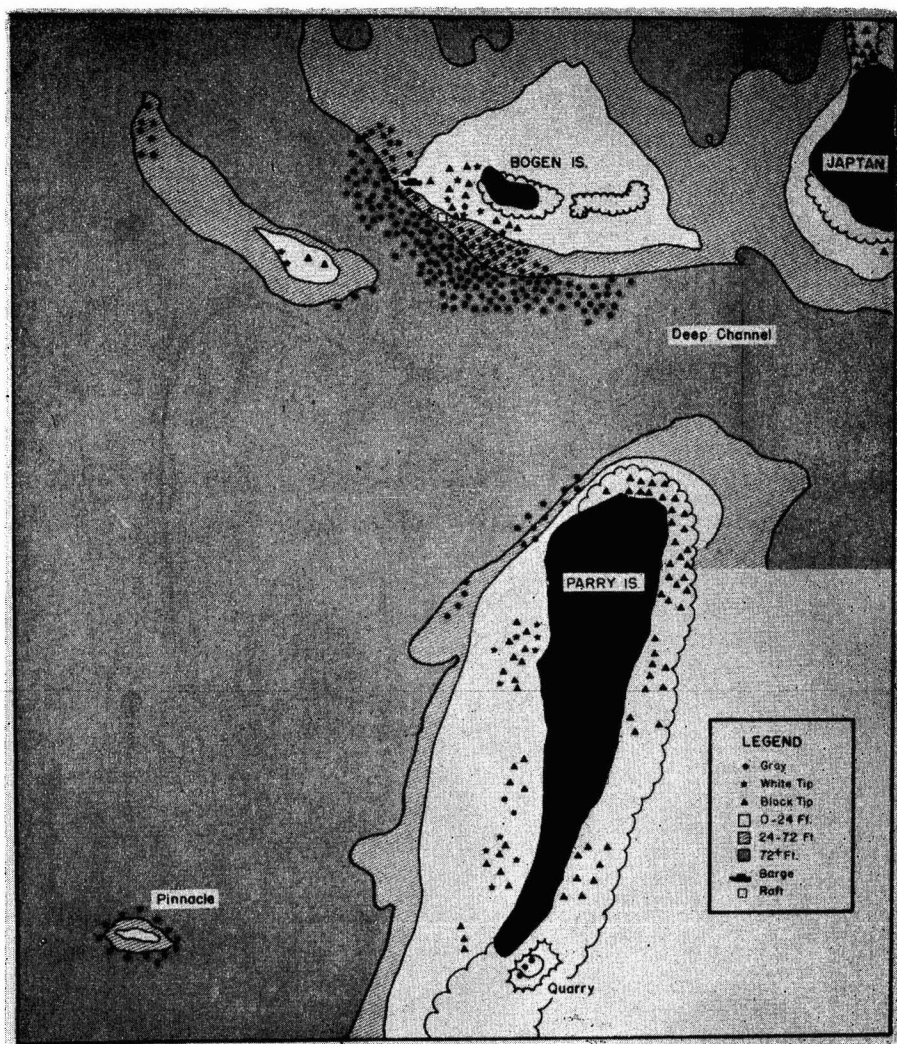


FIG. 5. Area in the vicinity of Parry Island, showing the sharks sighted during the period 26 July to 26 August, 1960, and indicating species involved and depth of water where sighting occurred.

Parry Island and the depth of water in which these sightings occurred. Two basic rules were observed in making this count: (1) no more than one count was made in any one area on any one day; (2) if there was any question of whether or not a particular shark had already been counted on any one day, then this shark was disregarded. This survey was not intended to show shark abundance, but rather to illustrate the areas and depths in which each of the three species was normally seen.

The distributional picture which emerges is consistent with the observations made throughout the program. For example, during 2 months of work in 15 ft of water off Engebi, only two grey sharks, both approximately 2 ft in length, were seen. On the other hand, the experiments involved many blacktips and whitetips. In contrast, when experiments were conducted along the edge of the dropoff into Deep Channel, both whitetips and greys were in abundance, while blacktips were only occasionally seen.

In December 1959, while fishing outside the seaward reef slope at Palmyra, we saw only grey sharks, finding these in considerable abundance. At the same time, only blacktips were common on the reef flat a hundred yards away. We saw comparatively few whitetips at Palmyra, these in shallow water over the reef. Klausewitz (1959) found these same species occupying similar habitats in the Red Sea.

Exceptions to this general distribution pattern were noted. Large grey sharks appeared at poison stations in water scarcely 6 ft deep, while whitetips were seen swimming over open bottom, far from the nearest coral head or rock. Furthermore, Strasburg (1958) reports the catching of two blacktips at sea in the Marquesas.

BEHAVIOR AND HABITAT

The sluggish behavior noted in the whitetip is consistent with a life in and about the caverns and crevices of the coral reef. This species was noted as being clumsy and ineffective in attempts at taking baits which were suspended in midwater. However, this same shark was remarkably effective in tracking down and capturing prey which had taken shelter deep in one of the many holes or crevices typical of a coral reef, thus making available to it prey which are beyond the reach of both greys and blacktips. Considerable time was spent placing wounded fish far back into small holes in the reef and then watching as a whitetip appeared, nosed about tentatively for the correct hole, and then swam in and captured its prey. Large whitetips were seen disappearing into small holes from which they presently emerged, always head first. The experiment described below involved whitetips and greys and illustrates the division of the food source between these two species.

Experiment 1

Three small wounded fish, each essentially identical, were presented simultaneously at three positions below the raft at the edge of Deep Channel, where water depth was approximately 35 ft: (1) Suspended mid-way between surface and bottom; (2) on the bottom in an exposed position; (3) concealed in a hole beneath a large rock on the bottom.

Bait 2 was lowered to the bottom at the end of a weighted line. Baits 1 and 3 were both secured to a single line which ran from the raft, down under one side of the rock, through the hole, out the other side and back up to the raft. By alternately hauling in one end of the line or the other, both baits could be simultaneously hauled aboard the raft or lowered into position.

The experiment was repeated 16 times when both greys and whitetips were in the vicinity. Although the two species seemed equally adept at taking the exposed bait on the bottom, the suspended bait in all but one instance was taken by a grey, while the whitetips completely monopolized the bait concealed in the hole.

When grey sharks encountered humans in shallow water they often started and fled in much the same manner described for the blacktip, rather than exhibiting their usual relatively bold inquisitive approach. Possibly this apparent change in behavior was a result of their being out of their usual habitat. This observation might offer an insight into the characteristically timid behavior of the blacktip. Perhaps this apparent timidity is an adaption of these relatively large animals, which must remain in motion, to a shallow water habitat. The shark, unable to take shelter and without room to maneuver, may find flight the alternative. In the blacktips, this characteristic timidity is more apparent in the larger individuals. The suggestion that this behavior might have some survival value implies the existence of a natural predator. The only evidence we found of such a predator was the presence of an 18-inch blacktip in the stomach of an 80-lb grouper.

DETECTION AND CAPTURE OF FOOD

Sharks are well known to feed avidly on dead fish, meat, and many other food materials dumped as garbage or used as bait. It is also well known that they will consume living fish impaled on a hook or spear. These, however, are unnatural situations. Undoubtedly, under natural conditions these sharks will feed on such prey as may have been killed or weakened by disease or injury. The sharks in the Eniwetok lagoon, as elsewhere, are highly responsive to stimulus situations which suggest injured and/or distressed, as well as dead or moribund

prey. Nevertheless, it seems unlikely that this source of food alone is sufficient to support such a large shark population. It seems probable, then, that they act not only as opportunistic scavengers, but also as predators on healthy free-moving animals. Eibl-Eibesfeldt and Hass (1959) report observing both *C. menisorrhoe* and *C. melanopterus* in the Indian Ocean herding schools of mullet against the shoreline and actively feeding on these fishes. Similarly, Strasburg (1958) observed pelagic whitetips (*Pterolamiops longimanus*) herding squid under a night light. Strasburg also cites other evidence of pelagic sharks apparently capturing what would appear to be highly motile elusive prey.

We observed no such activity among the three species in the lagoon at Eniwetok. These sharks seemed oblivious to the presence of the numerous reef fishes which were continually present during the shark's patrolling activities. This behavior might be expected, however, as only under such conditions would the reef fishes allow sharks to move in amongst them without exhibiting immediate alarm and taking shelter. This same apparent oblivion to what appears to be potential prey is also standard behavior seen in many other reef predators, for example the groupers, snappers, and moray eels. It seems likely that this behavior on the part of the predators is advantageous in allowing them to catch their prey unawares with a frequency which, while sufficient to maintain life, does not destroy the illusion of their non-aggressiveness. It is also probable that the threshold for the release of feeding on healthy prey fluctuates with the relative availability of more readily obtainable food items, such as dead or disabled fish.

The present study is confined to feeding behavior with respect to dead, damaged, and distressed prey. An effort is made to determine which of several sensory modalities are involved and which are dominant in the sequence of events between initial stimulation and the act of consuming the prey.

RESPONSE TO OLFATORY STIMULI

A number of experiments were conducted which elucidated the role of olfaction in detect-

ing dead and living prey. Only three (II, III, and IV) will be reported in detail.

Experiment II

This experiment was designed to study the response of these sharks to an uninjured fish struggling on a line, which might thus produce visual, mechanical, auditory, and perhaps olfactory cues.

The glass-bottom boat was anchored in 40 ft of water on the steep slope of Deep Channel where the current ran in one of two directions, depending on the tide. Ten trials were conducted, each at a time of strong flood or ebb current when visibility was good. As a precaution against the sharks becoming conditioned to feeding at this location, the trials were spaced over a period of several weeks, with only one trial on any one day. Each trial involved one fish, either a grouper (Serranidae), snapper (Lutjanidae), or mullet (Mugillidae), 2 to 3 lb in weight, secured to a line by a piece of soft, light cord which passed through the membrane behind the maxillary. The fish had been caught by barbless hook and kept in tanks at the laboratory until needed; they appeared to be healthy and uninjured.

Before the fish was lowered to a point 5-10 ft above the bottom, a 5-min observation period was conducted to insure that no sharks were in the area. If sharks were seen the test was delayed until at least 5 min after they had disappeared.

Observations included species of shark, the time each took to locate and take the bait, its general behavior, and particularly the nature and direction of its approach. It was presumed that if the sharks approached directly and consistently from downstream the attracting stimulus had been initially olfactory, inasmuch as only the olfactory stimulus was affected by the current. If the approach was from random directions, then other sensory cues, such as visual, were likely to be involved in the initial attraction.

The results are summarized in Table 1. In 9 of the 10 trials the sharks appeared from downstream, swimming rapidly and directly toward the bait, thus indicating they were responding to olfactory cues carried by the current. The

TABLE 1
RESPONSE OF SHARKS TO FISH WHICH ARE STRUGGLING ON A LINE (EXPERIMENT II)

TRIAL	BAIT	TIDAL CURRENT	NO. AND LENGTH OF SHARKS INVOLVED	TIME TO APPEAR	DIRECTION FROM
1	mullet	flood, moderate	1 4-ft grey	17 min	downstream
2	mullet	flood, strong	1 4-ft grey	10 min	downstream
3	grouper	flood, moderate	2 6-ft greys	15 min	downstream
4	snapper	flood, moderate	2 4-ft greys	20 min	downstream
5	grouper	flood, moderate	1 6-ft grey	18 min	downstream
6	mullet	flood, moderate	1 4-ft grey 1 6-ft grey	5 min	downstream
7	mullet	ebb, moderate	2 4-ft greys	10 min	downstream
8	grouper	flood, moderate	1 4-ft grey 1 3-ft whitetip	16 min	downstream
9	grouper	ebb, moderate	2 6-ft greys 1 6-ft whitetip	14 min	downstream
10	grouper	ebb, moderate	2 4-ft greys	25 min	upstream

one test which might at first glance appear to deviate from this pattern deserves quotation from the field notebook:

Introduction was made at 1035 . . . bait positioned 10 ft off the bottom, being carried 20-30 yd astern by the current where it struggled vigorously until 1050 when noticeably tired. By 1055 bait no longer struggled, but simply maintained position, looking quite natural. At 1100, two 4-ft grey sharks appeared from upstream, cruising slowly along the bottom toward the test area and giving no indication of having sensed bait. When still about 20 yd upstream of the boat (and 40 ft down, on the bottom) they both became noticeably alerted. At this point apparently they had become aware of the boat on the surface, as they veered upward and swam at an accelerated rate directly to within 5 yd of the boat, turned aside at this distance and circled twice. Then, seeming to lose interest, they returned slowly to the bottom and continued at their leisurely pace downstream, passing within 10 yd of the bait without apparent notice (as stated, the bait was not struggling, but merely maintaining position in the current). The sharks continued downstream approximately 20 yd below the bait, at which point they both obviously and simultaneously became alerted, turned around, and with increasing speed raced back upstream straight toward the bait, with one of them taking it.

The first response in the above observation was apparently one of vision to the boat on the surface. The second response, in which the sharks returned upstream to the bait, was obviously one of olfaction.

In this experiment, the sharks appeared to be following an olfactory cue in a direct line to an uninjured fish. However, there was no as-

surance that other stimuli were not also involved in the detection and approach to the bait. The question arises whether these sharks can follow an olfactory cue directly to its source in the absence of other cues.

The classical experiments of Parker (1914), in which he observed the approach of dogfish to bait when both nostrils were free and when one was occluded, has been offered as proof that directional response to olfactory cues is possible by virtue of the ability of each nostril to detect minute differences in the concentration of odorous material. In standing water in the ponds at Coconut Island we have observed the hammerhead (*Sphyrna lewini*) describing the typical figure 8 pattern, described by Parker, in which the shark is apparently locating the source of stimulation by continually turning toward the nostril exposed to the greater concentration of the material. Tester (1963) also describes how blinded blacktips spiral down from above in converging on bait on the floor of the tanks at the Eniwetok Marine Biological Laboratory. It seems likely that sharks are capable of following an olfactory trail in running water, particularly when the current is strong and the trail narrow, thus forming what would essentially be an olfactory corridor. Under such conditions they could be expected to make a direct-line approach by taking advantage of the normal lateral movements of the head, which are part of the swimming motion, in keeping themselves oriented in the stimulus trail.

Experiment III

The purpose of this experiment was to determine if these sharks are capable of orienting themselves in a current and following an olfactory corridor in a direct line to its source in the absence of other stimuli.

A location on the edge of Deep Channel similar to that used in Experiment II was chosen. Essentially clear, colorless fish extracts were used as the olfactory cues. These were prepared from several species of grouper but always of the same concentration (600 gm of fish flesh or skin macerated in a Waring blender with 6 liters of fresh water and diluted in a large plastic container with 64 liters of sea water). The material was introduced from the glass-bottom boat by siphoning from the container through a clear plastic $\frac{3}{4}$ -inch hose which ran down to the top of the reef. From here it continued down the slope through a series of holes to a small cave at the base of a large rock. The hose was thus effectively concealed for a distance of approximately 30 yd from the cave.

Eight tests were conducted under various velocities of tidal current over a 15-day period

with no more than one trial on any one day. Each test was preceded by a 30-min control period during which any unusual behavior in sharks sighted was noted. The duration of the introduction varied according to the response of the sharks. Observations included the species and general behavior of the sharks and particularly the direction and nature of approach. The results are given in Table 2.

A consistent response was exhibited by both grey and blacktip sharks during this experiment. In the presence of a current they appeared from downstream, swimming at an accelerated rate directly to the mouth of the cave where, in most cases, they briefly stuck their snouts inside. They then turned in very small circles here for a short period of time before returning slowly, in a random manner, downstream. After an initial approach by any one shark, this same shark often reappeared and repeated the above described pattern several times. However, upon the third or fourth approach by the same shark, this shark often reversed direction 5–10 yd short of the hole and returned downstream without the characteristic circling.

TABLE 2
RESPONSE OF SHARKS TO EXTRACTS OF FISH FLESH OR SKIN (EXPERIMENT III)
(All Sharks Came from a Downstream Direction)

TRIAL	EXTRACT	TIDAL CURRENT	NO. AND LENGTH OF SHARKS RESPONDING	TIME TO INITIAL APPEARANCE	TOTAL INTRODUCTION TIME
1	frozen flesh	ebb, moderate	1 6-ft grey 1 4-ft grey 1 4-ft whitetip	10 min	1 hr
2	frozen flesh	flood, moderate	1 4-ft grey 1 5-ft grey 2 4-ft whitetips	12 min	1 hr
3	frozen flesh	ebb, moderate	1 4-ft grey 1 5-ft grey	25 min	30 min
4	frozen flesh	ebb, weak	1 4-ft grey 1 4-ft whitetip	35 min	1 hr
5	frozen flesh	ebb, weak to moderate	1 4-ft grey 1 4-ft blacktip 1 5-ft whitetip	16 min	45 min
6	frozen flesh	flood, moderate to strong	3 4-ft greys 1 4-ft whitetip	9 min	45 min
7	fresh flesh	flood, strong	2 6-ft greys 1 4-ft grey 1 4-ft whitetip 1 5-ft whitetip	7 min	30 min
8	fresh skin	flood, moderate to strong	3 6-ft greys 1 4-ft grey	6 min	30 min

It might be suggested that the olfactory stimulus had not itself been directional, but that the sharks, having been alerted by the olfactory cue, had simply turned upstream, and oriented to the current. However, while a rheotactic response may have influenced the shark in its initial decision as to which way to go in the corridor, this observer does not feel that the response observed could have been directed by such a cue. Among other considerations, in an approach directed solely by current the shark would have at least briefly overshot the source of the olfactory stimulus. This would have resulted in a brief but certainly noticeable period of uncertainty as the shark turned back to pick up the olfactory cue once again. Nothing of this sort was seen. Furthermore, the following of an olfactory corridor was observed in the absence of current and will be described shortly.

Occasionally the extract elicited a response from other fish in the area which could have provided an approaching shark with supplementary cues. However, in only 2 of 27 observed approaches might this source of error have affected the results.

When the current subsided, the approach of the sharks immediately became less direct—illustrating the importance of the current in maintaining the definition of the corridor. No new sharks appeared during slack water and those already present milled about continuously within 30 yd of the cave. Approaches to the cave during slack water were made in a random manner and from all directions. At this time it was apparent that the material was diffusing out in all directions from its source and was at the same time being retained in the immediate area.

The whitetip did not seem to be as responsive to the introductions as were the blacktip and the grey. On several occasions whitetips swam directly to the cave in the manner noted in the grey and blacktip. However, whitetips just as often swam past the hole without any noticeable response to the extract. As apparent unresponsiveness has been noted as characteristic of the whitetip, it is difficult to draw any direct comparisons between this species and the grey and blacktip from the observed behavior.

Whitetips do have the ability to follow an olfactory corridor. The following quotation from

the field notebook describes an incident which clearly illustrates this and also the formation of a corridor in the absence of current:

A large parrot fish (*Scaridae*, 10 lb.) was speared in about 20 ft. of water. The fish tore itself from the spear and took shelter in a large coral head. Within 1 min. a 5 ft. whitetip appeared. It became obvious that the shark had sensed the presence of the wounded fish as it poked about the holes of the coral head and then swam into one of them. The chase which followed was witnessed from the surface. The two fish could periodically be seen through one or another of the many holes which honeycombed the coral head. First the parrot fish would flash by and then the whitetip in pursuit. The coral head contained an extensive network of caves and the chase seemed to take advantage of most of them. Suddenly the parrot fish emerged from a hole. Apparently it had temporarily eluded the whitetip because there was no immediate sign of the shark. The parrot fish swam off rapidly on a straight course for about 30 yd. where it made a 90° turn and continued on the new course, in a straight line, until it was out of sight. The whitetip emerged from the hole just seconds after the parrot fish, but already its prey was out of sight. The whitetip circled briefly, then started out along the same path taken by the parrot fish. When it arrived at the point of the 90° turn it continued on a few yards, but quickly slowed and turned around. After another brief period of circling the shark picked up the second leg of the trail and followed it straight out of sight.

In this instance, the corridor was formed by olfactory substances given off by the moving wounded fish. There was no noticeable current at the time.

The sharks involved in Experiment II had apparently been initially alerted by an olfactory stimulus emitted by a fish which, while in distress, was uninjured.

The ability of these sharks to detect the presence of an unwounded fish in a state of stress through an olfactory cue was noted by Tester (1963) early in the program. This point has been neglected since the observations of Sheldon (1911), in which a dogfish was noted to locate an undamaged crab wrapped in eelgrass. However, in Sheldon's experiment the attracting stimulus (or stimuli) may have been a movement or sound made by the crab instead of, or in addition to, an olfactory stimulus. Any conclusions derived from Experiment II are open to the same criticism. Another source of criticism might be the assumption that a fish with a line passing through its maxillary membrane may be considered uninjured. The ex-

TABLE 3

RESPONSE OF SHARKS TO WATER CONTAINING A GROUPER UNDER STRESS (EXPERIMENT IV)
(All Sharks Came from a Downstream Direction)

TRIAL	TIDAL CURRENT	NO. AND LENGTH OF SHARKS RESPONDING	TIME TO INITIAL APPEARANCE	TOTAL INTRODUCTION TIME
1	flood, moderate	2 5-ft greys	15 min	30 min
2	ebb, strong to slack	3 4-ft whitetips	5 min	30 min
3	flood, moderate	1 4-ft grey 1 3-ft whitetip	10 min	1 hr

periment described below was designed to minimize these sources of error.

Experiment IV

This experiment was conducted to determine if these sharks are capable of detecting and tracking down, exclusively by olfaction, an uninjured fish under stress.

The experiment was carried out using the procedure described for Experiment III, except that, in place of the extract solution, the large plastic container was filled with sea water and contained an uninjured grouper (1-10 lb) which was presumably under stress. In each case, the fish was caught by line with a barbless hook. During the experiment the fish was agitated intermittently with a pole, using care not to inflict any damage, while the water was running from the container to the bottom as described for Experiment III.

Three trials were conducted over a period of 10 days, with at least 3 days between each trial. The results are given in Table 3.

The response was essentially the same as that to the extracts in Experiment III. Greys and whitetips were involved in the experiment; no blacktips were seen.

The captive grouper obviously emitted an olfactory stimulus which attracted the sharks upstream to the cave. Critics of this experiment may question whether a recently hooked fish can be considered uninjured. There is justification for pointing out the hook wound as well as the skin rubbed and mucus dislodged during handling. These factors offer a possible source of error. However, the results were consistent with findings in the laboratory tanks where it was possible to maintain considerably more control

over experimental conditions. In the latter tests (Tester, 1963) the strength of the stimulating olfactory component varied with the degree of distress of the fish being used. It appeared that a maximum level was reached shortly after the death of the fish.

It has been shown that the sharks were able to track down a distressed but apparently uninjured fish by olfaction alone in Experiment IV. Although they could also have made exclusive use of the olfactory sense in tracking down the hooked fish in Experiment II, it is highly unlikely that they did so. We shall see that, in all probability, other sensory modalities not only contributed to, but in fact dominated, certain phases of the approach.

RESPONSE TO COMPRESSION WAVES

Compression waves are regarded by many to have an important effect on the behavior of sharks, both as an attractant and as a repellent. Wright (1948) claims that attack patterns in sharks are released by sounds. Many investigators (e.g., Eibl-Eibesfeldt and Hass, 1959) report that the vibrations and sounds made by a wounded fish will attract sharks. On the other hand, some sounds have been reported to have a repelling effect, as for example the underwater shouts of divers (Hass, 1951). These reports are based on incidental encounters with sharks and are generally complicated somewhat by the presence of stimulating factors other than compression waves which might themselves have been influential in eliciting the observed response. For example, Wright's conclusion is based to a considerable degree on observations of sharks appearing just after an underwater explosion to feed on the dead and stunned fish.

The presence of the disabled fish is mentioned almost incidentally, although in such a situation it is impossible to dismiss the olfactory and visual cues emitted by these fish. Similarly, the presence of olfactory and visual cues also complicate reports of sharks being attracted to a struggling fish in response to compression waves. In regard to the repelling effect of the shouts of divers, we did not see any such response in the species studied in Eniwetok. However, sudden movements and/or a sudden burst of bubbles from the aqua-lung, such as might readily accompany a shout, often startled the blacktip and put it to flight.

It is important to consider the ability of sharks not only to sense these stimuli but also to locate their sources. Parker (1912), investigating sound as a directing influence on the movements of some teleosts, noted that there was a directing effect only during the duration of the sound. These results cast some doubt on the ability of such noncontinuous stimuli as a single underwater explosion to attract sharks.

Two experiments on the perception of compression waves by sharks were conducted in the field at Eniwetok.

Experiment V

The aim of this experiment was to investigate the effects of compression waves of a variety of sonic frequencies on these sharks. The following were presented:

A. Continuous pure tones, covering a frequency range in steps from 100–1,000 cycles per sec.

B. Sounds of mixed frequencies recorded on a circular tape, including:

1. wood struck against wood, 1/sec and 6/sec;
2. rock struck against rock, 2/sec and 6/sec;
3. rasping effect, continuous;
4. rattling of nuts and bolts in a bottle, continuous.

C. Shouts by the observer, directly projected through the apparatus.

The experiment was conducted at the Engebi location, using a tape recorder equipped with an underwater speaker lowered 6–8 ft below the surface. Each sound was presented during 20-min trials, with each trial immediately following a 20-min control period and conducted

under two sets of conditions: (1) following a different experiment in which sharks had been drawn into the experimental area and were still present, and (2) upon arrival at the site, with no sharks present. All sounds were audible to a submerged human at distances greater than 150 ft.

Although we watched closely for signs of any sort of response, for example curiosity, we saw nothing in the behavior of the sharks which suggested that they were able to perceive the sounds.

Experiment VI

This experiment was designed to investigate the effects of various subsonic compression waves on these sharks.

A metal hoop, having a diameter of 36 inches, was fitted with a rubber diaphragm held in position by a series of surgical tubing lacings. This piece of apparatus was installed midway through a natural tunnel, approximately 20 ft long, in the coral ridge bordering Deep Channel beneath the raft. A line was secured to the center of the diaphragm on that side facing away from the channel, and this line was run out of the tunnel and up to the surface where a small skiff rode at anchor. The diaphragm could thus be vibrated by jerking on the line.

Two trials were conducted in which the diaphragm was vibrated irregularly for a period of 20 min immediately following another experiment in which a number of grey sharks had been drawn into the area and were still present. Throughout both trials there were grey sharks swimming about calmly in the area. At times they passed within 5 yd of the tunnel's entrance.

In observations from the raft we looked for any type of response in the sharks which might indicate that they were aware of the vibrating diaphragm. We saw no such response.

The negative results in these two experiments do not mean that the sharks could not perceive these stimuli. If releasers of feeding activity are emitted by struggling fish in the form of compression waves, they probably are of a specific nature or involve a characteristic pattern. It would have been a rare stroke of luck if we had duplicated a specific releaser with our crude experiments. The problem of delimiting the

sensory capacity for stimuli of this sort is probably best approached with conditioned response experiments on captive sharks under controlled conditions before attempting to establish their role in feeding behavior under natural conditions.

Although the work of Parker (1903, 1911), Kritzler and Wood (1961), and others has demonstrated that at least some sharks are sensitive to compression waves of a relatively wide range of frequencies, it has yet to be proven experimentally that such stimuli normally release feeding behavior. Nevertheless, incidental observations at Eniwetok indicated they do play an integral role in feeding activity. These observations are of a nature similar to those mentioned at the beginning of this section and are subject to the same reservations. One such observation is quoted from the field notebook:

... A 30 lb. grouper was speared on the slope bordering Deep Channel ... the grouper fled, dragging the spear, into a small cave. ... Within seconds, 5 greys 4-7 ft. in length swam excitedly into the area from downstream. As soon as they were in the area, however, their excited state diminished. They swam about in the area for several minutes, appearing to steadily lose interest, before slowly drifting off downstream and out of sight. After a few minutes ... 5 greys made another approach which seemed as highly motivated as the preceding one. Immediately I looked below to see a small puff of sediment emerge from the cave—the grouper was obviously thrashing about inside. Almost as soon as the sharks were in the area, all became quiet in the cave, whereupon the sharks immediately lost their excited state and settled down to cruising about as before. Two 4-ft. whitetips joined them before they all again drifted off downstream. After a few minutes ... another small puff of sediment was visible at the mouth of the cave—the grouper was struggling again. I quickly looked downstream to see the greys on their way in as before. The pattern previously described was repeated, but this time there were 4 whitetips (3-5 ft.) in addition to the 5 greys. Several minutes after the sharks disappeared downstream for the third time the grouper scrambled out of the hole and, dragging the spear, struggled along the bottom toward the bigger, more protective caves farther up the slope. The 5 greys charged into the area from downstream before it had gone 20 ft. At this point, the grouper stopped, and ceased all movement. Although the grouper was in a completely exposed position, the excited state of the onrushing greys diminished almost as soon as the grouper stopped moving. Instead of attacking the completely vulnerable grouper as I expected, the greys settled down to swimming slowly and randomly about the area. Often they came within inches of the mo-

tionless grouper, and on at least one occasion grazed it. The 4 whitetips rejoined the group, along with 2 blacktips (3 and 4 ft.) making a total of 12 sharks, all obviously interested, but offering no show of excitement or indication that they regarded the wounded grouper as prey. Nevertheless, the sharks did not gradually drift off downstream as they had previously, but continued to swim about in the area. Thirty minutes later, when we had to leave, the situation was unchanged—the grouper was still sitting motionless in the same spot, while the 12 sharks swam slowly about. Most of this random swimming about the area, both at this point and earlier, had occurred downstream of the grouper.

It was significant that all approaches and departures, as well as most of the random swimming in the area, occurred downstream of the grouper. This indicated that olfaction was involved throughout the incident. Although the excited approach of the greys during this incident appeared to coincide with the periods when the grouper was struggling, it is possible that they had first been conditioned by an olfactory cue. In this case, the olfactory cue may have had a threshold lowering effect for the postulated compression wave stimuli. At least one author (Wright, 1948) doubts that olfaction alone will release attack patterns in sharks. In this latter regard, blinded sharks in the tanks fed avidly on chunks of fish flesh which were lying on the bottom, thus offering little other than olfactory stimuli before the sharks came into contact with them. The question here is whether or not the behavior of these blinded sharks can be considered normal.

While the sharks in the latter phase of the incident did not attack the wounded grouper, they did not drift off downstream as they had done when this same fish was concealed in the cave. We are probably safe in assuming that the behavior pattern demonstrated in swimming slowly about in the area was appetitive in nature. This suggests that an additional stimulus was required to release the actual attack. This is to say that a combination of stimuli, e.g., an olfactory element and erratic motion might have been necessary to release the attack in this case. The olfactory cue may have simply released an exploratory behavior pattern which drew the sharks to the area. Once there, the release of the attack may then have required a specific stimulus not presented by the quiet, natural looking grouper, the coloration of which blended

in very well with the bottom on which it was resting. The cessation of movement by this grouper upon the approach of the sharks may have been a well-established protective behavior pattern. We will consider this incident further in the next section. During a later period of the study, a grouper of the same species and approximately the same size was caught at the raft where the underwater action was witnessed from the observation cage. The grouper wrapped the line about a piece of coral and by the time the line was freed and the struggling fish hauled toward the surface, a single 5-ft grey came rushing into the area from downstream. The shark went directly for the struggling fish, took the tail section into its mouth, and with a few vigorous lateral shakes of its head came away with the after portion of the fish.

There is no doubt that rapid erratic movements are a prime releaser of attack patterns in these sharks, particularly in the presence of specific olfactory cues. Many authors have noted an excited state in sharks resulting from the sensing of movement (for example Limbaugh, 1958). As both a mechanical disturbance and a visual stimulus are usually produced by a moving object underwater, it is very often difficult to say with certainty which is more significant as a releaser of attack in a given situation.

On one occasion, while fishing for sharks, a 3-ft grey was hooked in the presence of five larger greys. As the shark struggled vigorously on the line, the other five sharks became highly active and appeared to be chasing the hooked animal. Initially we supposed that an attempt was being made to attack the hooked shark, but upon landing this individual after several minutes of activity we noted no evidence of injury. If the larger sharks had been attempting to feed on the smaller hooked shark there is no doubt that they could have done so. It is probable that the activity of the hooked shark excited the others which were then simply following the focal point of this activity. Inasmuch as other species of fish, similarly hooked and struggling, were immediately taken by the grey shark there is a suggestion here that this species of shark is inhibited in some way from attacking members of its own species. This possibility is further supported from observations made while fishing for snapper (*Lutjanus bohar*) at Palmyra. Grey

sharks drawn to the fishing area showed no interest in the many free-swimming snapper, but would immediately attack a snapper which became hooked and began to struggle on the line. Contrariwise, although the sharks would swim rapidly about one of their own species which was hooked and struggling, no attacks were observed.

RESPONSE TO VISUAL STIMULI

Contrary to many reports on the subject (for example Halstead, 1958) vision was found to play a major role in the feeding activity of the sharks in the Eniwetok lagoon. We briefly mentioned vision above in regard to instances involving movement. The following experiments were designed to further clarify the role of vision in cases where there was little or no movement of the bait.

Experiment VII

The object of this experiment was to determine the role of vision in these sharks when they are approaching a motionless bait up an olfactory corridor.

Two baits of similar appearance were prepared for each trial, one of which was a 4-inch cube of grouper flesh while the other was a 4-inch cube of wood. After we were confident that no sharks were visible in the area, the two baits were presented together in a strong current, suspended 3 ft apart, midway between the surface and the bottom. Observations were made from the cage, and a record was kept of which bait was hit first, as well as of the nature and direction of approach of the sharks.

Experiment III had shown that these sharks are capable of orienting on an olfactory stimulus in a current and swimming directly to its source. In every case during the present experiment the sharks appeared from downstream, swimming at an accelerated rate, presumably following an olfactory trail emitted by the grouper flesh. If the sharks had continued to orient exclusively on the olfactory stimulus all the way to the bait, then the fish would presumably have been taken in all trials. This, however, did not occur. In 20 trials conducted over a period of 2 days, the fish was struck first 11 times while the block of wood was hit first 9 times. As no preference was

shown, it seems that at least the final phase of the approach was visually directed.

When the shark selected the wood, the object was either simply bumped or briefly taken into the mouth and then rejected. No teeth marks were found on the wood following the test. In all cases the fish-baits were carried away. Only grey sharks were involved.

If we accept as fact that these sharks orient visually during the final phase of their approach to a motionless prey, we must then question the nature of the stimulating visual image, bringing us to the subject of visual acuity.

Most elasmobranchs reportedly possess an all-rod retina with a high ratio of visual cells to ganglion cells, which provides for low visual acuity. While this would presumably result in an inability to see objects in detail, the sharks would be able to utilize their visual sense under conditions of relatively little light (Gilbert, 1961). Kato (1962) found no evidence of cones in the retina of blacktips or whitetips. Perhaps even more significant, he found no specialized area, corresponding to the human fovea, which is generally assumed to be associated with visual acuity.

At Engebi, we often noted that sharks attracted by a dead fish suspended on a line often struck objects in the immediate vicinity of the bait before taking the bait itself. A rock about 1½ ft square, which was situated in the middle of a sandy area below the baits, as well as floating seaweed and a lead weight on the line a foot above the bait were often tested with a nudge or by actually being taken momentarily into the mouth. These observations suggest one of two alternatives: (1) these sharks lack the visual acuity necessary to distinguish the visual appearance, i.e., form, markings, etc. of fish from inedible objects in the immediate vicinity; or (2) although these sharks do possess the visual acuity necessary for such a distinction, it was not utilized by them in this situation.

Tester and Kato (MS) showed that small blacktips and greys have the ability to discriminate between a number of objects of different shape, e.g., squares, triangles, and rectangles, and that they make this discrimination from a distance of at least 6 to 12 ft. These species then possess at least the degree of visual acuity required to discriminate between these forms.

The following experiment was an attempt to detect evidence of the utilization of a high degree of form discrimination ability in the feeding behavior of these sharks.

Experiment VIII

This experiment was designed to determine whether or not the visual cues offered by a fish through its characteristic morphological features are significant attractive visual stimuli to these sharks.

Two fresh dead fish were selected for each trial, both being of the same species, but one a little larger than the other. Three species were used: goatfish (Mullidae), 8 trials; surgeon fish (Acanthuridae), 3 trials; and squirrel fish (Holocentridae), 10 trials. The larger fish was then decharacterized by removing the head and all the fins, reducing it in size to approximately that of the smaller, still natural-appearing fish. A long, deep incision was then made along the ventral side of the natural-appearing fish to insure that olfactory stimuli emitted by both baits were essentially the same. The baits were both secured to a single line, one spaced approximately 18 inches above the other, with their respective position being reversed on alternate trials. After assurance that no sharks were visible, the baits were suspended motionless at a point midway between surface and bottom in a strong current. Observations were made from the cage and a record was kept which bait in the pair was taken first, along with the species of shark involved and the nature and direction of approach.

It was assumed that if the characteristic morphological features which had been removed from one of the pair were significant as attractive visual stimuli, then the natural-appearing fish would be favored in the initial choice made by the sharks. This in turn would demonstrate a high level of form discrimination ability in these sharks. However, no apparent preference was shown to either of the two bait types in 21 trials. The decharacterized fish were hit first 11 times, while the natural-appearing fish were hit first 9 times. Once both baits were hit simultaneously. The relative positions of the baits on the line had no apparent effect, with the top bait being hit first 9 times and the bottom bait

11 times. As in Experiment VII, only grey sharks were involved and these approached in every case at an accelerated rate from downstream. By positioning the bait in mid-water we favored this species. A number of whitetips were seen about the bottom at various times during the trials.

The baits introduced during this experiment were the first food given by us to the sharks in over a month, with the exception of a few uninjured living fish. This is an important consideration in this experiment, as any conditioning of the shark population to feeding on our presentations would have resulted in a tendency to take our offerings indiscriminately. However, no conditioning was noted at this stage of experimentation.

The failure of these sharks to show a preference for the natural-appearing fish over the one which had been reduced to a simple object suggests that the visual appearance of a fish per se is not itself significant to these sharks when feeding. When the results of this experiment are considered along with the observations at Engebi already mentioned, in which the sharks struck at inedible objects in the immediate area of the baits, it appears that the significant visual cue in these cases was simply that of an object within the immediate area of the source of the olfactory stimulus. This evidence suggests that these sharks do not utilize a high degree of visual acuity in their feeding activity. It follows, then, that if the visual stimulus is not moving, it must otherwise contrast with the background against which it is viewed in order to provide an effective visual cue.

The following experiment involves the relative effectiveness of two objects in attracting the attention of sharks, when these objects differ from one another in degree of contrast in brightness with their background.

Experiment IX

This experiment was designed to determine which of two baits, one white and the other black, would be taken first when both are presented to these sharks together at the surface.

Paired 3-inch cubes of fish flesh (parrot fish, snapper, and grouper) were used as bait in this experiment, with members of each pair identical

except that one retained its natural white color, while the other was dyed black with nigrosine dye. It had been previously determined that nigrosine dye was not sensed by blinded sharks in the tanks.

The experiment was conducted at the raft over 40 ft of water when a current was running. A wounded grouper was placed in the cage until a number of sharks had been drawn about the raft. The fish was then removed from the water, allowing the source-point of the olfactory stimulus to be carried off downstream and taking the sharks with it. When the sharks were about 20 yd downstream from the raft, the two baits were dropped into the water, spaced approximately 10 ft apart. Movement of both baits was negligible as they slowly settled. At times the response of the sharks immediately followed the entry of the baits into the water, indicating that the splash had been sensed; at other times the response was noted after the baits began to sink, indicating a visual response. These responses followed the introduction too closely to have been those of olfaction. In either case, the sharks came racing back upstream and in all cases the baits were taken before they had fallen 10 ft. The bait taken first in each case was recorded, although the alternate bait was always taken almost simultaneously. As it was anticipated that the amount of incident light present would influence the results, trials were conducted under different light conditions, with from 10 to 56 trials held each day for 4 days.

The results under each of the different sets of conditions prevailing were as follows: (1) daylight with clear sky, in 96 trials black was taken 79 times, or 82%; (2) daylight with overcast and drizzle, in 21 trials black was taken 15 times, or 71%; (3) daylight with overcast and heavy rain, in 14 trials black was taken 8 times, or 57%; (4) after sunset, with clear sky but almost dark, in 41 trials black was taken 32 times, or 78%. The total: for 172 trials under all conditions, black was taken 124 times or 72%.

As the sharks, all greys, raced back toward the test area they were viewing the baits against light surface water. The black bait, then, contrasted with its background to a greater degree than did the white bait. This was as noticeable

to the observer sitting in the cage as it obviously was to the sharks.

Recalling some of the observations made earlier, we might consider again the speared grouper which rested motionless on the bottom while 12 sharks swam slowly about in its immediate area. Although this grouper was in a completely exposed position, its coloration blended in well with the bottom on which it was resting. In this position the grouper was apparently at least temporarily safe from attack by the 12 sharks, in spite of the fact that it was wounded and still emitting the olfactory stimulus which presumably had released the appetitive behavior pattern which these sharks were at that time demonstrating. At Engebi, the sharks struck at the rock which was sitting in the middle of the sandy area, floating seaweed, and the lead weight—all inanimate objects in the immediate area of the bait, but all of which sharply contrasted in brightness with the backgrounds against which they were viewed by the sharks. These results are consistent with the conclusions drawn by Gilbert (1961) from anatomical studies of the shark eye.

Although there is little doubt that vision is the predominant directing sense within the visual field, the effective distance involved here will be highly variable. Such external factors as water clarity, incident light, and whether or not the prey is under cover, no doubt determine the effectiveness of vision in any given situation.

RESPONSE TO GUSTATORY AND TACTILE STIMULI

While lack of visual discrimination apparently led to selection of the wood as often as it did the fish during Experiment VIII, the shark was quick to learn its error. Initially the wood was actually taken into the mouth, but after one or two successive trials a nudge was generally sufficient to dismiss the inedible object. An appraisal of the bait by the visual or olfactory sense may have been the basis for the nudge, but when the bait was taken into the mouth, other senses, e.g., gustation and/or tactile sense, undoubtedly came into play.

A review of the gustatory sense of sharks is presented by Tester (MS). In this review, he points out that while the receptors of the gustatory

sense (e.g., taste buds or terminal buds) occur in the skin of the body, fins, and barbels of many species of fishes, in the elasmobranchs they appear to be associated with papillae which are confined to the epithelial lining of the mouth and pharynx. He also calls attention to the claim of Budker (1938) that the "pit organs" located on the body of elasmobranchs have a gustatory function.

An effort was made to design an experiment which would illustrate the respective roles played by both gustation and the tactile sense in accepting or rejecting food taken into the mouth. As the block of wood in Experiment VIII differed from the fresh fish in tactile cues as well as those of olfaction and gustation, it was impossible to say which of the two might have been more influential in the rejection of the wood.

An attempt was made to synthesize a bait which possessed the visual and tactile properties of acceptable bait, but which lacked the olfactory and gustatory properties. Tester et al. (1955) concluded that in the flesh of many fishes there is present a substance or substances which, when extracted with alcohol or water, can be perceived by a fish through its sense of smell or taste and which promotes the urge to feed. Tester commented (personal communication) that extraction by alcohol was effective in removing this substance from a piece of flesh. He observed that squid prepared this way was not detected by blinded blacktips and although taken into the mouth by normal blacktips, they were subsequently rejected. He attributed this rejection to the lack of acceptable gustatory stimulation, in as much as the texture of the prepared squid seemed to be similar to untreated squid.

The following experiment was an attempt to duplicate Tester's results in the field.

Experiment X

This experiment was designed to determine whether or not a bait offering the visual and tactile stimuli of food, but which lacks the olfactory or gustatory stimuli, will be acceptable as food by these sharks when they are actively feeding.

A number of 3-inch cubes of grouper flesh

were prepared. Half of these baits were soaked for 4 days in each of the following concentrations of ethyl alcohol: 35%, 75% and 95%, in that order. After the alcohol treatment the baits were soaked in sea water for 3 hr. It was hoped that the product of this process would be a bait which felt and looked like food, but did not taste or smell like food. In actuality, however, the texture of the product was not identical to that of normal flesh, being notably dry and leathery. The experiment was nevertheless continued, with each of the treated baits being paired with a normal bait. It was assumed that the normal bait would be taken. If the treated bait was also taken this would indicate that the wood in Experiment VIII had been rejected due to its tactile properties rather than its lack of acceptable olfactory or gustatory stimuli. If, however, the treated bait was not taken, Tester's results would be confirmed and it would appear that gustation (and perhaps the tactile sense too) had been involved in the rejection of the wood.

The test was carried out at the raft, in a moderate current, using essentially the same technique described for Experiment IX, except that in this case all 15 trials of the experiment were conducted during a 30-min period of one afternoon and the response to both baits was noted.

Only grey sharks were involved in the results. The treated bait was hit first 6 times, while the natural bait was hit first 9 times, indicating that the sharks did not make a distinction between the visual appearance of the two baits. All the baits were taken into the mouth, but although in all trials the natural bait was swallowed immediately, the treated bait was rejected within seconds. As this rejection took place after the bait had been taken into the mouth, it appeared to be based on gustatory stimulation (if we are correct in assuming that the bait offered acceptable tactile stimulation). A snapper was seen taking, and apparently retaining, one of the treated baits rejected by the grey shark.

Another effort to clarify the roles played by gustation and the tactile sense in feeding involved the use of sponges. It was thought that perhaps a sponge which had been soaked in an extract of fish flesh would be accepted by the sharks as food. If this were the case, then by pairing the soaked sponge with a normal sponge

it would have been possible to present a choice of baits which posed the same problem to the sharks as did Experiment X. In order for the experiment to have been a success, however, it was necessary for the sharks to have accepted the soaked sponge as food, and this proved to be only temporarily true. Initially, the soaked sponge was carried off in the manner seen with a chunk of fish, while the plain sponge was rejected as was the prepared bait in Experiment X. However, after 3 trials the sharks began to lose interest in the soaked sponges until they either dismissed them after an unenthusiastic nudge, or ignored them completely. Furthermore, as the sharks learned that the soaked sponges were inedible, the extract no longer excited them. In this latter regard it is difficult to say whether the sharks actually learned that the extract did not indicate food or whether olfactory fatigue was the major factor.

A definite change in general behavior of the grey sharks was first noted during Experiment IX and became very evident during Experiment X. As the sharks became conditioned to feeding about the raft they responded instantly to any object which was presented. In addition, there was a sharp increase in the number of sharks responding to our test situations. Where initially a maximum of 5 or 6 grey sharks were involved in our experiments, the number steadily increased during this period of increased food supply until more than 20 were being drawn about the raft. The initial population had been relatively stable and through successive observations involving experiments which utilized minimum feeding, it had become possible to recognize a certain group of about 6 individuals that appeared day after day. These same individuals were seen after the population numbers increased, but apparently many other sharks which normally frequented other areas were drawn to this point of concentrated feeding. This change involved only grey sharks, which is understandable as this species was completely monopolizing the additional food. The increase in numbers of sharks resulted in a markedly increased element of competition. When we witnessed the simultaneous rush at the baits by up to 10 sharks, it was understandable that all baits were taken into the mouth before any discriminations were made as the slightest hesitation by

a shark in this situation immediately eliminated it from a chance at a bait. Fortunately the present tests, which required concentrated feeding, were concerned with probing questions which did not suffer from these effects. This change in behavior, along with the increase in numbers of the local sharks, was therefore viewed with interest rather than alarm.

FOOD PREFERENCES

Sharks have been popularly described in a general way as creatures with an exceptionally voracious appetite, feeding on such unlikely objects as tin cans, bottles, and other trash (Lineaweaver, 1960). Although considerable effort was brought to bear on the problem of food preferences during this study, the experiment described below was the only one, of many experiments conducted, which clearly indicated a preference for one of two food materials presented.

Experiment XI

This experiment was an effort to determine whether or not these sharks show any preference between grouper flesh and the flesh of various species of mollusks, e. g., *Tridacna* sp., (10 trials); *Spondylus* sp., (5 trials); and *Cassus* sp., (3 trials).

Mollusk flesh in 2-inch cubes was paired with chunks of grouper flesh of the same size, with both baits thus offering an essentially identical visual appearance. Prior to the test, large pieces of grouper and mollusk flesh of the species to be tested were placed in the cage on the raft to attract sharks. When the introductions began, there were 10 grey sharks, 3 to 6 ft in length, present in the area. The method of introduction was as used in Experiments VIII, IX, and X, except that all trials were conducted during one session. Observations were made to detect any evidence of a preference which might be shown between the two baits.

The fish baits were hit first 8 times, while the mollusks were hit first 9 times, indicating that there was no visual preference. However, although both the fish and mollusks were taken into the mouth with equal vigor, the fish were presumably swallowed while the mollusks were rejected almost immediately. The results were comparable to those of Experiment X, with the

response toward the mollusks similar to that shown toward the treated bait. On one occasion a single shark took the *Tridacna* and then the grouper. After a short period, with both baits in its mouth, the shark rejected one, presumably the *Tridacna*. These same rejected baits were subsequently taken by groupers and snappers which waited below the feeding sharks. Although the mollusks tested were unacceptable as food by these sharks, it is known that they will feed readily on squid.

It was possible, therefore, to observe a preference when one of the bait-choices offered was unacceptable to the sharks. However, when both bait-choices presented were acceptable, it became difficult to make this distinction, even though one might have been significantly more attractive than the other. Thus, most of our experiments concerning food preferences yielded inconclusive results. For example, a test might have been conducted to determine the comparative attractiveness of two baits, A and B, both motionless and presented on the lines within 10 ft of each other. As indicated in Experiment VIII, although these sharks might have been drawn in by an olfactory stimulus produced by bait A, they would then have been quite likely to have hit B inasmuch as the final phase of the approach to the bait would have been visually directed. Once having taken bait B, this bait would be retained as long as it was not actually unacceptable.

It has been noted (Tester, 1963) that some types of fish flesh appear to be more attractive to sharks than do others. In the ponds at Coconut Island the notably dry-fleshed snapper, *Lutjanus gibbus*, appeared to be far less desirable to captive sharks as food than did the much juicier tuna, *Katsuwonus pelamis*. Springer (1958) also noted this preference for tuna. Is it possible that this apparent preference is actually due to a higher concentration of some basic attractant which is common to the flesh of both fish? It has become increasingly apparent that some substance (or substances) in fish flesh is perceived by the sense of taste and/or smell of these sharks which is a powerful element in the release of a highly motivated feeding pattern. Furthermore, it was indicated in Experiment X and also in the work of Tester et al. (1955) that this substance could be ex-

tracted from the flesh, whereupon the flesh itself was left undesirable to the sharks. Tester et al. (1955) expended considerable effort in attempts at purification, fractionation, and identification of the attractant extracted from fish flesh which released a response in captive tuna. While the precise identity of the substance eluded the investigators, many of its chemical properties were determined and presented by the authors. Tester et al. (1954) suggest that the so-called attractant which is present in the body juices of fish, squid, shrimp, and other forms may be a substance (or substances) which is common to all these forms.

FEEDING DETERRENTS

The recent increased interest in the habits and behavior of sharks has stemmed largely from a growing awareness of the need to develop a more effective means of protecting humans from shark attack.

A number of tests of proposed repellents were conducted, including a test of the repellent now in general use by the armed services. The results of some of these tests illustrate many of the problems involved in producing an effective repellent.

Experiment XII

This experiment tested the effectiveness of the standard shark repellent (copper acetate-nigrosine dye) in protecting both dead and wounded fish from attack by these sharks.

The experiment was conducted at two locations: (1) on the bottom at the edge of Deep Channel, and (2) from the raft. In the tests on the bottom, involving whitetips, three baits were tied to packages of repellent and anchored on the bottom, while seven baits, without repellent, were anchored nearby. In the tests from the raft, which involved grey sharks, all the baits were tied to packages of repellent and lowered halfway to the bottom. No attempt was made to attract sharks before beginning these tests.

The whitetips took all of the unprotected baits but did not take any of those tied to the packages of repellent. On the other hand, although the first grey to appear during the tests at the raft occasionally exhibited a slight hesi-

tation when making its approach, it was never long before several greys were in the area and the bait and repellent package were quickly taken together. The repellent packages were shortly rejected, but there was no indication of a subdued appetite. One grey was seen swimming away trailing a black cloud of shark repellent from its gills with no show of discomfort.

The relative effectiveness of the repellent in protecting the baits from the whitetips may be related, at least in part, to the absence of the group feeding effect in this species. This effect, which was discussed earlier, was noted to lower the threshold for the release of feeding patterns in grey sharks.

Experiment XIII

In this experiment the standard shark repellent was presented as a large cloud, both by itself and as a protective screen for various attractants. Trials were conducted at the raft in which 30 gm of repellent were dissolved in 64 gal of sea water in a plastic container. This solution was presented alone as well as mixed with each of the following attractant materials: (1) two small macerated goatfish, (2) 500 ml fish extract, (3) 1,000 ml of fish extract, and (4) 2,000 ml of fish extract. The extracts were prepared by using 50 gm of grouper flesh per 500 ml of fresh water.

The presentation was made by simply pouring the contents of the container into the water after a number of sharks had been drawn in about the raft and noting the results. In each case, a cloud approximately 6 ft deep and 12 ft wide formed at the surface next to the raft and slowly drifted downstream.

When the plain repellent cloud was introduced, the sharks rapidly converged on the cloud to a distance of approximately 5 yd where they circled slowly, following the cloud as it drifted downstream. After a few minutes, however, the sharks lost interest in the cloud and returned to the raft. When the repellent cloud containing the macerated goatfish was introduced, the fish fragments sank beneath the cloud where they were quickly taken by the sharks. The sharks, then excited, swam unhesitatingly up into the cloud where they circled vigorously. Sixteen

greys, 3–6 ft long, were involved in the first two phases of this experiment.

The response to the repellent clouds containing the extract solutions was essentially the same in each case. After rapidly approaching the cloud, the sharks circled briefly about its edges and then moved slowly inside without notable excitement. Within 5 min of introduction, all sharks had lost interest in the introduction. Eight greys, 3–6 ft in length, were involved in these tests.

It seems noteworthy that the extract elicited an unexcited pattern of exploratory behavior rather than the highly excited aggressive behavior seen following the introduction of macerated goatfish. In any case, the most that can be said for the repelling qualities of the material used in this test is that the sharks did not swim into the cloud without incentive to do so. It may theoretically have served to conceal an otherwise attractive visual stimulus which might have been inside.

Experiment XIV

This experiment tested the effectiveness of an underwater light suspended on a line in protecting dead fish.

The apparatus was designed so that the bait (dead goatfish) was suspended 2 ft below the light in a position where both could be viewed from the underwater chamber. Observations were then made of the response of the sharks to the bait, both in the presence and in the absence of light. Tests were conducted during four different nights using both 110- and 300-watt bulbs. A steady light was used, as well as a light which flashed at rates of approximately 15, 35, and 50 flashes per min. Periods of light, 20 min long, were alternated with 20-min periods of darkness during both of which the baits were presented. Sharks had been drawn to the area by bait placed in a wire basket which was suspended in the water and then raised prior to each test. A strong current was flowing toward Deep Channel during each test.

Initially the steady light was effective in protecting the bait from the sharks for the entire 20-min period, with the bait being taken soon after the light was extinguished. During the early periods of light the sharks milled about

at the edge of the field, consistently downstream of the bait and light. Upon continued contact with the light the sharks became progressively bolder until despite the light, flashing or steady, they showed little hesitation in taking the bait. This boldness seemed to increase notably with the number of sharks present. There were usually between 5 and 10 grey sharks present during these tests; no other species was seen. This test proved to be a good illustration of progressive loss of apprehension through growing familiarity with an initially strange situation, as well as the mutually stimulating effect of some species of sharks on one another in certain situations.

CONCLUSIONS

1. Three species of sharks are common in Eniwetok lagoon: the grey shark, *Carcharhinus menisorrh*; the blacktip shark, *C. melanopterus*; and the whitetip shark, *Triaenodon obesus*.

2. Each species inhabits a rather characteristic habitat within the lagoon: (a) the blacktip in relatively shallow water (1–40 ft approx.) over sand and coral rubble flats which extend out from shore for distances ranging from a few yards to several miles; (b) the grey, along the outer slope of these flats, in deeper water and in the passages to the sea; and (c) the whitetip about rock-ledges and coral heads.

3. The feeding behavior of these sharks shows differences which in many cases appears to be associated with their characteristic habitats.

4. Blacktip and grey sharks show a marked increase in excitement when feeding in numbers. This phenomenon, often referred to as a "feeding frenzy" in extreme cases, does not seem to occur in the whitetip.

5. All three species are highly sensitive to stimuli emanating from or suggesting injured and/or distressed, as well as dead or moribund prey.

6. These sharks can detect, by olfaction, both injured fish and uninjured fish in a state of stress.

7. Olfaction is the most effective sense in detecting prey at a distance, providing the olfactory stimulus has had sufficient time and means for effective dispersal.

8. These sharks are able to follow an olfactory stimulus quickly and directly to its source without benefit of other orienting stimuli when the olfactory material has been drawn out as a narrow trail by a strong current or, in standing water, when the source of the olfactory stimulus is moving.

9. Generally, olfactory stimuli are effective in releasing a highly motivated pattern of exploratory behavior in grey sharks, which is appetitive in nature. Consummation of the feeding act then requires a subsequent specific stimulus, as for example one of vision.

10. The grey shark is often highly excited by, and attracted to, the source of rapid and/or erratic movement. The effect is intensified in the presence of certain olfactory stimuli but is not dependent on their presence.

11. Despite displaying varying degrees of initial curiosity toward many unusual stimulus situations arising in their environment, the sharks exhibit caution when encountering a situation which is unfamiliar. This caution will steadily subside, however, with an increasing familiarity with the situation.

12. The final phase of approach to a motionless prey by the grey shark is normally directed by vision, even though the feeding pattern may have been initially released by some other sensory modality, for example, olfaction.

13. Although vision is an important sense in the feeding activity of these sharks, a high degree of acuity and form discrimination is not demonstrated. Rather, the significant visual cues seem to involve the detection of movement or contrasting brightness, or both.

14. These sharks may attack any object which they sense in a high concentration of an olfactory material.

15. The grey shark rejects, from the mouth, food which does not permit acceptable gustatory stimulation.

16. The standard shark repellent (copper acetate-nigrosine dye) now in use by the armed forces is ineffective in preventing the grey shark from swimming into a cloud of this material when the species is present in numbers and is motivated by food within and adjacent to the material.

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